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THE FUNCTIONAL RESULTS OF MUSCLE TRANSPOSITION IN THE HIND LIMB OF THE RAT

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SIX FIGURES

Most of our knowledge concerning the functional adjustment of transposed muscles is derived from cases of muscle transposition for the correction of motor paralyses in the limbs of human beings. The investigation of these clinical cases which has been confined primarily to the question simply of whether readjustment is or is not possible has brought forth the following principles, as formulated by Scherb ('38), regarding the possibility of reeducation after muscle transposition.

In the arm learning follows the transposition of any muscle to compensate for any other non-synergic muscle, provided the operation is mechanically successful. In the leg learning is likewise universal for slow voluntary movements. But for automatic walking movements, reeducation after a muscle is transposed so as to act antagonistically to its normal function may be prevented reflexly by the remaining function of any muscle of the group for which the transposed muscle is supposed to compensate. Even in the case of walking movements, however, learning can be expected to follow if all of the muscles

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for which the transposed muscle is substituted are completely paralyzed.

Extremely little is known about functional adjustment of transposed muscles in the common laboratory animals. Marina ('12) reported that after transplanting the insertions of opposing pairs of ocular muscles in monkeys there was an immediate adjustment in the action of the transposed muscles to produce coordinated eye movement. Olmsted, Margutti, Yanagisana ('36) repeated the experiment on cats, dogs, and monkeys, and also reported a rapid functional adjustment which they interpreted as being due to a short training period. Dusser de Barenne and de Kleyn ('29) found that four out of eight rabbits displayed normal horizontal and vertical nystagmus movements of the eye immediately after transposition of the internal and external rectus muscles. They did not attribute this to a functional adjustment, however, since they found further that after excision of all six ocular muscles the remaining retractor bulbi muscle alone was capable of effecting these movements.

Anokhin ('35) states that after transplanting part of the M. extensor quadriceps femoris to a flexor position in the hind leg of the cat, the transposed portion of the muscle, as indicated by the cat's walking coordination, changed its function to a flexor, but that when the muscle was prepared after 5 months training for kymographic recording, the transplanted portion on reflex stimulation contracted synergically with its counterpart as a normal extensor. He interpreted the adjustment as being due to a "dynamic rearrangement" rather than to a fixed change in central nervous relations. Taylor ('36) crossed the Achilles tendons between the hind legs of the frog and contradicted Manigk's ('34) earlier report on the same experiment in saying that there was no immediate adaptation in the function of the crossed muscles. He also sewed the Achilles tendon to a flexor position in the same leg and found no immediate adjustment. The frogs were not kept to determine whether or not a change would occur in time.

The above reports on the effect of muscle transposition thus vary on two points: first, in regard to whether functional adjustment does or does not occur, and secondly, if it does occur, whether it follows gradually as the result of a learning process or whether it occurs immediately by means of automatic reflex accommodation.

A number of cases (Flourens, 1842; Osborn and Kilvington, '10; Rawa, 1885) in which the cross-suturing of nerves to antagonistic groups of muscles in the limbs of dogs, pigs, cats, rabbits, fowls, and guinea pigs resulted apparently in a gradual return to normal coordination might be taken to indicate that the experimentally reversed functional relationship of antagonistic muscles is readjusted by means of learning in these animals. Kennedy ('14), on the other hand, states that restoration of function occurred at once after crossing nerves to flexor and extensor muscles in the foreleg of the dog without any evidence of a reeducation period. The work of Weiss ('36 b), however, has shown that the return of normal coordination after the crossing of limb nerves in amphibians is a phenomenon quite different from either learning or automatic reflex adjustment. In the absence of more conclusive evidence that the same is not also true of the higher vertebrates, one cannot be sure that the effect of nerve crossing is comparable to that of muscle crossing as a criterion of learning or reflex adjustment.

Because of the scarcity and inconsistent interpretation of data on the functional results of nerve and muscle crossing in mammals, and the important implications of such data for the analysis of central nervous function, a reinvestigation of the problem was undertaken, using the rat and creating conditions more critical than previously attempted in the laboratory or obtainable in clinical studies. This paper deals primarily with muscle transposition, cases of nerve crossing being mentioned only as mechanical controls.

Antagonistic flexor and extensor muscles of the hind foot were transposed to discover whether or not there would be an immediate adjustment in coordination on recovery, and if not,

whether adjustment might be brought about in time as a result of reeducation. The albino rat was used because of the large amount of information already available on the behavior and learning capacities of this animal.

The antagonistic muscles of the shank causing plantar and dorsi-flexion of the foot were chosen for study because their normal function is clearly antagonistic and their contraction produces a simple movement that is easily observed, frequently and indispensably involved in the animal's general activity, and readily subjected to natural training situations. Furthermore, since the nerves and nerve tracts concerned are relatively accessible, any adjustment that might occur would be open to further analysis by means of deafferentation, cord transection, and brain stimulation and excision.

THE OPERATION

The tendons of the two main dorsi-flexors of the foot, the M. tibialis anterior and the M. extensor digitorum longus, were cut and inserted together onto the Achilles tendon of the heel so that in their new position contraction of the muscles produced plantar flexion instead of dorsi-flexion. In order to provide more room for these muscles in their crossed position, the small fibula bone and the interosseous membrane were removed entire. The large lateral gastrocnemius muscle inserting normally on the Achilles tendon and producing plantar flexion of the foot was pulled forward, its tendon cut and sutured to the distal end of the extensor digitorum longus tendon so that its contraction in this position caused dorsi-flexion of the foot instead of plantar flexion. The diagrams in figure 1 indicate the essential part of the operation.

Every other muscle of the shank except the M. peroneus longus was removed as follows: After freeing the individual tendons distally and cutting them low down in the ankle, the muscles were pulled proximally and separated cleanly from the surrounding tissues. Then after cutting their nerves and blood vessels and severing the muscles from their origins the entire muscles were lifted out. In this way all the main nerves

and blood vessels in the leg and foot were left intact except those supplying the extirpated muscles.

The M. peroneus longus was left in place between the transposed muscles to help prevent adhesions between them. Its action is mainly that of eversion and does not obscure the reversed plantar- and dorsi-flexor action of the transposed muscles. But because of Scherb's statement that the action of a single remaining antagonist muscle may reflexly inhibit reeducation, the M. peroneus longus was also removed in all

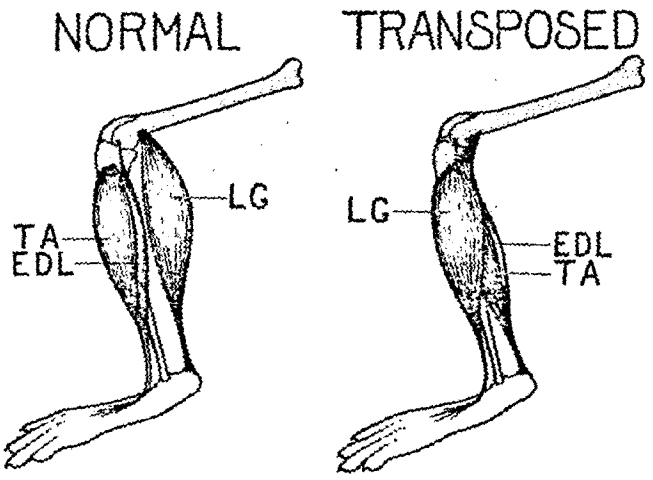


Fig. 1 Diagram illustrating the transposition of flexor and extensor muscles of the foot to produce reversal of foot movement. TA, M. tibialis anterior; EDL, M. extensor digitorum longus; LG, M. gastrocnemius lateralis.

cases by a second operation after the first had healed. This removal of all associated shank muscles thus presents the best condition for readjustment, and also clarifies for study the action of the transposed muscles.

The operations were all performed under sodium amytal anesthesia with a single lateral incision from the upper thigh down to the ankle. The tendons were sutured with fine silk thread. Silk thread was also used in sewing the lateral gastrocnemius muscle to the fascia along the proximal part of the tibia bone to hold it in place and in suturing together the

fascia of the biceps femoris muscle which it is necessary to cut in the operation.

RECOVERY

On coming out of the anesthesia the animals held the operated leg behind them off the floor. After a few days when the swelling caused by the operation had subsided, the leg was held in a more normal position and some weight was put on it. In about 2½ weeks, depending on the neatness of the tendon sutures and the age of the animal, the foot began to show active movements which gradually became stronger. These movements from the beginning were in the reversed direction.

It soon became obvious that rapid recovery of normal coordination as reported for transposed ocular muscles, does not occur in these transposed limb muscles of the rat. After complete healing and regeneration of the tendon, pinching of the toes to elicit the withdrawal reflex produced flexion of the hip and knee joints as usual but plantar flexion of the foot instead of the normal dorsi-flexion (see fig. 4 b). When the rats tried to lift the foot in walking, the foot instead of rising with the knee, jerked downward so that the toes scraped along the floor. In the supporting phase of locomotion when the foot would normally be somewhat flexed in the plantar direction to support the weight on the toes with the heel off the floor, the foot was flexed dorsally with toes up in the air and the weight back on the heel (see fig. 6 b). When the animals attempted to rise upright on their hind legs and toes, they went back on their heels and the toes swung up in the air (fig. 5 b). When, in climbing, they tried to dorsi-flex the foot forward and upward, the foot extended downward and backward in extreme plantar flexion (fig. 2 b)—and so on, all the normal active movements of plantar and dorsi-flexion of the foot were in reverse.

In a number of the animals there was no recovery or only partial recovery of foot movement due to adhesions, ankylosis, slipping of the silk sutures, etc. These animals were all dis-

carded and only the nine rats to be described here, showing complete free movement of the joint through approximately the normal 170 degrees, were retained to determine whether or not the reversed foot movement could in time be adaptively modified by reeducation.

The further history of the leg movement in these animals can be summed up briefly here in saying that there was no sign of any functional adjustment whatever in the action of the transposed muscles. In view of the literature on muscle transposition in man and that on the cross suturing of nerves in the hind limbs of lower mammals, it was somewhat surprising to find that the reversed movements in these rats persisted

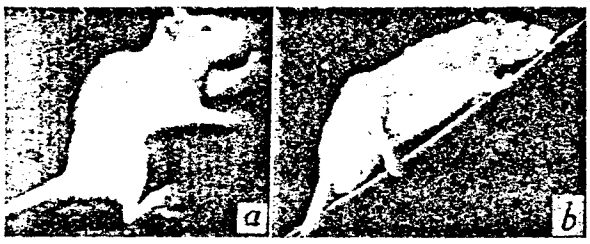


Fig. 2 Photographs showing foot posture resulting from reversed action of transposed muscles.

(a) When anti-gravity muscles of the leg contract to support the animal's weight, the foot, instead of pressing downward against the floor, flexes dorsally.

(b) When leg is lifted upward in climbing, instead of rising upward and forward with the knee, the foot pulls downward and backward in extreme plantar flexion.

without change, that the rats were incapable of learning not only to use the transposed muscles to advantage but even to inhibit the old contraction patterns which, with the muscles in the crossed position, were a distinct hindrance in much of their activity. Although six of the rats were kept longer than 13 months after the operation, readjustment failed to occur either in locomotion and other common activities, or under various training conditions calling for single, slow, elementary foot movement.

TESTS

Nine rats (seven unilateral and two bilateral cases) were obtained which showed on recovery unrestricted movement of the operated foot. The youngest was operated at the age of 50 days, the others at ages ranging from 55 days to 12 months. No age difference appeared in the results.

The reversed coordinations were tested in a series of twelve specific reactions involving dorsi-flexion and plantar flexion of the foot. These reactions were reliably consistent in normal animals. Also in control animals (operated similarly to the experimental group with removal of all shank muscles except the lateral gastrocnemius and extensor digitorum longus which were left uncrossed) these test reactions were likewise consistent and very similar to the coordination of normal rats.

The following movements described as they occur in normal and control rats were used as tests for contraction of dorsi-flexor muscles: (1) Raising and bringing forward of the foot during the suspended phase of locomotion (fig. 6 a). (2) Withdrawal reflex in which the foot is pulled upward when the toes are pinched or pricked (fig. 4 a). (3) Holding of the foot in a flexed position during the scratch reflex. (4) Extreme

Fig. 3 Foot posture when rat is held up by the forequarters with hind foot just touching the floor. (a) Control, operated as for muscle transposition save that muscles were left uncrossed. (b) Muscles transposed. (c) Muscles transposed and nerves to the muscles crossed.

Contraction of the lateral gastrocnemius muscle produces plantar flexion of the foot in (a) and dorsi-flexion in (b). In (c) the nerve of the gastrocnemius muscle activates the anter. tibial and ext. dig. longus muscles whose transposed tendons produce plantar flexion of the foot.

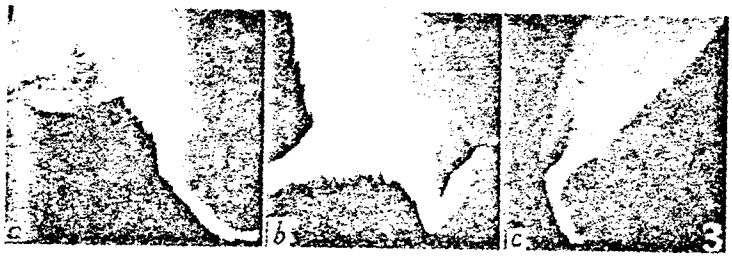
Fig. 4 Withdrawal reflex, (a), (b), and (c) as in figure 3.

The normal dorsi-flexion shown in (a) is reversed to plantar flexion after muscle transposition in (b) and counter-reversed back to dorsi-flexion again in (c) by the double operation in which the nerves are crossed as well as the muscles.

Taken from consecutive frames of motion picture film at 24 frames per second.

Fig. 5 Rising upright on the hind legs. (a), (b), and (c) as in figure 3.

Animals normally rise on toes and ball of the foot as in (a). In (b) the plantar flexion is reversed to dorsi-flexion so that the toes point up in the air and the weight falls on the back of the heel. In (c) the muscles somewhat weakened by incomplete reinnervation after nerve crossing do not lift the heel entirely off the floor as in (a), but if the body weight is somewhat lessened by partially lifting the animal as in figure 3 c the foot shows pronounced plantar flexion.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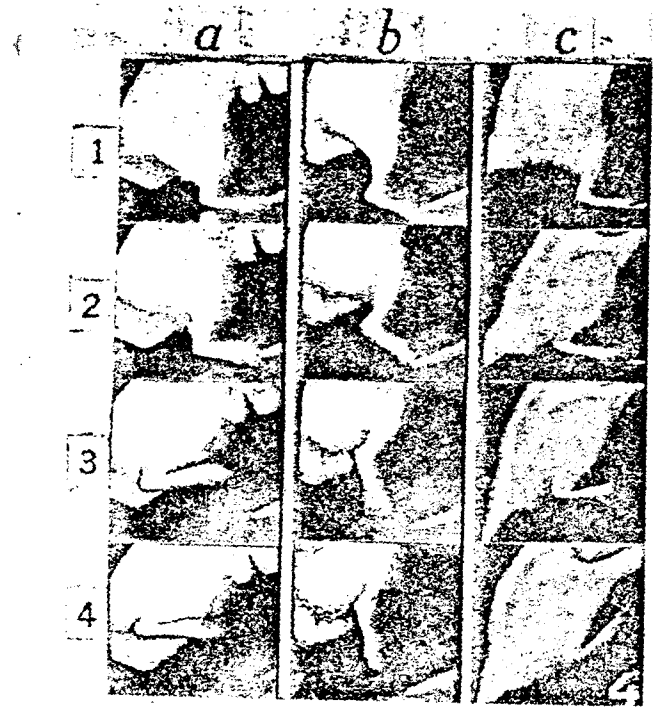
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lifting of the foot to clear an obstacle over which the animal is moving. (5) Escape movements when the rat is held down on its back by pressing across the abdomen. The foot is dorsi-flexed and brought forward underneath the restraining fingers. (6) Lifting of the foot in climbing a ladder, up the sides of the wire mesh cages, or over the edge of a wall.

In all of these reactions contraction of the dorsi-flexor muscles predominates over that of the plantar flexors resulting in dorsi-flexion of the foot. After transposition the muscles contract as before producing plantar flexion in the above tests instead of dorsi-flexion (figs. 2 b, 4 b, and 6 b).

The following responses shown by normal and control rats were used to test for contraction of the gastrocnemius muscle: (1) Supporting of the body weight on the toes and ball of the foot and pushing forward during the supporting phase of locomotion (fig. 6 a). (2) Placing of the foot when the rat is held upright by the forequarters with the hind foot just touching the floor. The foot is plantar-flexed, keeping the toes in contact with the floor (fig. 3 a). (3) Holding of the foot in a position to support the body weight when it is shifted to the hind feet in climbing a ladder and up the sides of the cages. (4) Braking action of the hind foot when the rat is dragged by the front legs slowly forward across the floor. The foot is pressed firmly against the floor and digs in if the substrate is soft. (5) Rising upright on the hind legs with the heels

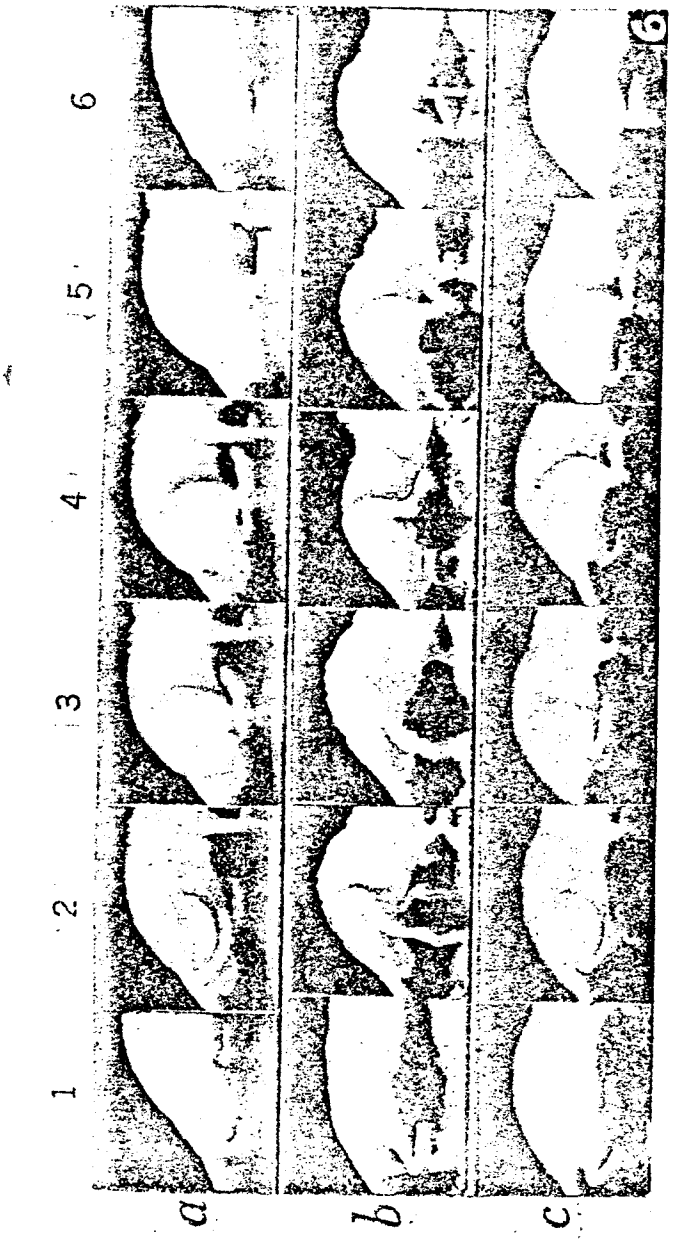
Fig. 6 Locomotion.

(a) Control, operated as for muscle transposition save that muscles were left uncrossed. As the knee is raised and brought forward the foot rises with it. When the animal's weight is shifted onto the foot in the supporting phase of the cycle, the foot is pressed downward against the floor.

(b) Muscles transposed. The foot, instead of rising with the knee, pulls downward and scrapes along the floor. In the supporting phase of the cycle, instead of pressing downward, the foot swings upward so that the weight falls on the back of the heel with the toes pointing up.

(c) Muscles transposed and nerves to muscles crossed. As in (a) the foot is dorsi-flexed in the suspended phase of the cycle and plantar-flexed against the floor in the supporting phase.

Figures taken from two successive cycles of locomotion. Where a rapid phase of the movement was blurred in the main cycle, a corresponding frame from the succeeding cycle was substituted.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off the floor and the body weight on the toes and ball of the foot (fig. 5 a). (6) Resting with the weight entirely on the hind legs while eating, cleaning, etc. The foot is pressed firmly flat against the floor.

In some of these tests, as in (3) and (6), the posture of the foot may be one of slight dorsi-flexion, but actually the gastrocnemius is contracting more powerfully than the dorsi-flexors to support the body against gravity. After transposition the gastrocnemius continues to contract in all of these tests causing a dorsi-flexion of the foot with the toes and ball of the foot swinging upward instead of pressing downward (figs. 2 a, 3 b, 5 b, and 6 b).

The rats were put through these test movements once a week for the first 2 months and monthly thereafter. Besides these test observations, considerable time was spent studying the rats' general activity in their cages, particularly their conduct in the special training situations. Moving pictures taken of locomotion and of some of the test reactions about 2 weeks after the return of function were compared with pictures taken 1 year later.

CHECKS AND CONTROLS

Clinical studies along with the work of Stewart ('37) have shown that disturbances in the muscle pattern produced by foreign innervation, paralysis, and tendon section can be compensated for, to a surprising degree, by so-called "trick movements" of associated muscles still in their normal condition. In the present cases this complicating factor was eliminated by complete removal of all the other muscles acting on the joint.

The reversal was not a passive movement produced by accessory tendons, fascia, pulling of the skin, or other mechanical factors. It disappeared after cutting the nerves or tendons of the transposed muscles. It did not occur on passive extension and flexion of the knee by manipulation under light anesthesia. The lateral gastrocnemius muscle is a two-joint muscle and is so attached in the normal animal that extension

of the knee results in passive plantar flexion of the foot. The possibility that extension of the knee might cause a passive dorsi-flexion of the foot after the muscle had been transposed was tested by mechanically extending and flexing the knee of the operated animals under light anesthesia. In no case did even extreme extension of the knee cause dorsi-flexion of the foot. In three cases it brought the foot into a neutral position at about right angles to the shank, but the foot was loose enough in these cases to be easily plantar-flexed with slight pressure. The two-joint action of the lateral gastrocnemius muscle had been successfully suppressed by fastening the proximal end of the muscle to the tibia bone in the operation (see fig. 1). The extensor digitorum longus is also a two-joint muscle, but the leverage effect on the origin is negligible so that passive flexion of the knee had no effect on foot posture. The possibility that knee action was exerting a slight pull on the muscles which, though not strong enough to manifest itself in actual movement of the foot, was enough to excite stretch reflexes and was thus producing the reversed movement, was tested by deafferentation. In the case so tested the reversal was unaffected by deafferentation of the limb. One of the three cases mentioned in which the passive pull of the gastrocnemius was noticeable when the knee was fully extended was reoperated and the origin of the gastrocnemius on the femur was severed and sutured to the fascia along the proximal end of the tibia thus making a one-joint muscle of the gastrocnemius. On recovery, the reversal continued as before until the rat's death 5 months later.

The reversal was not caused by an abnormal disbalance in muscle strength. It consisted of clear-cut reciprocal movements showing agonist contraction and antagonist relaxation as indicated by the following: The movement occurred distinctly in both directions, full plantar flexion and full dorsi-flexion appearing in turn in exactly the opposite phase in which they appeared in the normal controls. In cases where one of the muscles slipped loose and was removed leaving only the transposed muscle in place, then instead of a persistent

generalized flexion of the foot by the one muscle there occurred distinct active movement in one direction only with the foot hanging limp during the phase in which the missing muscle would have been contracting. Using two transposed muscles for plantar flexion to oppose only one for dorsi-flexion tended to maintain the normal strength relationship. Moreover, the leg of one control animal from which all the plantar-flexor muscles were removed except the small soleus muscle, which constitutes less than one-fifteenth the total mass of the plantar flexors and about one-fifth the mass of the transposed dorsi-flexors, was found to have fair coordination in the normal phase despite the extreme disbalance in muscle strength.

The crossed muscles were sufficiently strong to be used to advantage in normal coordination. That the crossed lateral gastrocnemius muscle was quite strong enough to produce dorsi-flexion is obvious because it did produce such movements. That the tibialis and the extensor digitorum combination was strong enough to support the weight of the rats is indicated by the fact that in control animals the single lateral gastrocnemius, somewhat less in mass than the combined tibialis anticus and extensor digitorum muscles, was sufficiently strong to raise the rat well off its heels when it rose upright on its hind legs. Even the small soleus muscle was capable of raising the heel off the floor in locomotion. Post mortem dissection of the rats showed that there had been no noticeable atrophy of the muscles and that they had been well adjusted so as to exert pull on the Achilles tendon during contraction. But even had the muscles been too weak to completely support the animals, one would still expect, had learning been possible, that there would have been some inhibition of the old contraction patterns which were more disadvantageous than no movement at all.

Tests for sensitivity several weeks after the return of function of the transposed muscles, along with dissection showed that the operations had been successful in preserving the nerve supply of the leg and foot. Slight pricking and pinching of the skin in all regions of the shank, foot, and toes

produced reflex reactions. Pressing the foot and bending the toes also caused reflex reactions. There was a small area in the ankle just anterior to the incision which in some cases was insensitive, but when tested 5 months later it too had regained its sensitivity. In two cases the incisions were opened 8 months after the operation. Reflex responses were elicited under light anesthesia by pinching the crossed muscles and even the tendons at the point of suture.

NERVE CROSS CONTROL

In one animal the nerves were crossed instead of the muscles, operation otherwise similar. The result was the typical reversal of foot movement characteristic of muscle transposition. In this control the reversal of foot movement was produced by a reversal of the sequence in which the muscles contracted without changing the insertions or otherwise altering the anatomical arrangement of the muscles. The dorsi-flexor nerves discharged into the plantar-flexor muscles at the time when dorsi-flexion normally would have occurred, and the plantar-flexor nerves activated the dorsi-flexor muscles when plantar flexion would normally have occurred. The retention of the nerve's original incidence of discharge for some time after regeneration into a foreign muscle is taken to be similar to that which occurs in adult amphibians as contrasted with the muscle-specific changes characteristic of younger animals (Weiss, '36 b).

CONTROLS WITH BOTH NERVES AND MUSCLES CROSSED IN THE SAME LEG

Finally a crucial test was made to show that the muscles in the transposed position were mechanically capable of producing the normal effects given the proper timing in their contraction. Two rats were prepared in which the nerves to the appropriate muscles were crossed and after allowing time for regeneration of the nerves, the regular muscle transposition was performed in a second operation. As a result of the double reversal these animals showed on recovery good

plantar flexion and dorsi-flexion of the foot in normal phase in all of the test reactions (see figs. 3 c, 4 c, 5 c, and 6 c). The double negative gave a positive effect. Reversing the action of the muscles without changing the incidence of their contraction reversed the foot movement, but when both the mechanical action and the timing of the muscles were changed to that of their antagonists by transposition plus nerve-crossing, then the transposed muscles worked just like the antagonists which they had replaced, resulting in normal coordination. These two control cases in which the foot was flexed and extended in normal phase to the animal's advantage by muscles transposed exactly as in the nine experimental animals showed conclusively that it was not any anatomical or mechanical aspect of the operation that was preventing readjustment. The lack of adjustment was apparently attributable only to a failure of the nervous mechanisms involved to undergo the necessary changes.

CONTROLS WITH ASSOCIATED MUSCLES LEFT INTACT

To make sure that readjustment would not occur if the associated muscles were left in place, two controls were prepared in which the anterior tibial muscle was transposed to the Achilles tendon and the lateral gastrocnemius was transposed to the extensor digitorum longus tendon and all other muscles of the shank were left intact except three small peroneal muscles, per. brevis, per. digiti quarti, and per. digiti quinti which it was necessary to remove to make room for the crossed tibial muscle. The intact muscles in these rats were strong enough to overpower the transposed muscles so that, although the foot movements were somewhat stiff and of less amplitude than normal, they were closer to normal than to reversed action.

That no adjustment of the transposed muscles occurred was indicated by the fact that after 3 months a partial ankylosis had set in due to the restricted movement of the joint. The legs were reoperated 6 months after the first operation and associated muscles removed to see if the reversed muscles

had undergone any adjustment in their action. In one case the tendon of the lateral gastrocnemius had become so encased to the tibia bone that it was immovable. In the other case the foot movements after recovery from the second operation were in reverse within the narrow limits of movement of about 40 degrees permitted by the partial ankylosis.

Another control was prepared in which all dorsi-flexor muscles were excised and the lateral gastrocnemius transposed to substitute for them, all other muscles being left intact. In this case readjustment would have required dissociation of the action of the lateral gastrocnemius from the other plantar flexors of the shank. As in the two controls above, the intact muscles over powered the transposed muscle so that it was mechanically lengthened in the correct phase of the coordination. The passive pull offered by the tonus of the transposed muscle kept the foot in a more normal posture than in cases where no opposing muscle was present. In a sudden shift from strong contraction of the plantar flexors to complete relaxation as may occur in the withdrawal reflex, the tonus of the transposed muscle brought the foot to a neutral position from extreme plantar flexion so that at first sight it appeared like active dorsi-flexion, but the presence of associated shank muscles and the mechanical lengthening of the transposed muscle in the correct phase of the movement had not resulted in any active adjustment after 6 months.

TRAINING

At first all nine rats were merely allowed to run about in their cages as usual in the hope that learning would occur without any special training. They were kept in groups of two to four in wire mesh cages measuring 45 by 63 cm. and 33 cm. in height, containing sawdust and excelsior. To make the rats more dependent on the operated legs, the contralateral hind foot (except in the two bilateral cases) was immobilized in a position of slight dorsi-flexion by operations causing adhesions and eventual ankylosis of the joint. According to Schorb (38) any condition that tends to break up the

inherent automatic walking pattern is helpful in bringing about voluntary control over transposed leg muscles.

As they moved about, the animals often paused with the foot in a supporting position, but always on extension of the hip and knee joints the toes would swing upward and the weight fall on the heel. In climbing through the excelsior the rats often caught the operated foot so that they had to stop and make special efforts to free it. The hind feet moved while the animals were licking them, and in the general course of their scratching, feeding, and playing about, all kinds of passive satisfactory and active unsatisfactory movement occurred which offered plenty of trial and error cues for the guidance of learning had the animals been capable of it.

When no improvement appeared in any of the animals after 2 months, special measures were taken to help induce reeducation. An attempt was made to train four of the animals to raise themselves off their heels with the transposed dorsi-flexors by placing food high in the cage where they would have to rise upright on their hind legs to reach it. Hard food was placed in a self-feeder against a smooth wall so that the front feet could not aid in reaching it. The food was raised gradually to a point so high that by resting on their heels and stretching upward to their utmost the rats could just barely nibble at it. It would have been greatly to the animals' advantage to have used the transposed muscles to raise themselves just ½ cm. higher to ease the strain on the rest of the musculature and permit them to get a good bite of the food. Had they been able merely to bring the toes down to the floor and balance on the sole of the foot, it would have given them a firmer footing. But after 3½ months of this training not one of the animals had learned to rise off its heel or to keep its foot flat on the floor. Figure 5 b shows the typical foot posture shown by the rats in rising upright for food. It was a common thing for the rats to balance on the contralateral heel and flex slightly the hip and knee of the operated leg in a sort of climbing movement. The foot was thus brought into a position of plantar flexion in contact with

the floor correctly placed for rising on the toes. The foot might remain there for some time with occasional slight movements as the rat stretched upward. It looked like a good start for learning, but every time the weight was shifted to this leg with contraction of the extensor muscles of the knee, the foot was dorsi-flexed and the toes swung upward. The control animals mentioned above with only two uncrossed muscles in the shank, one for plantar and one for dorsi-flexion, rose easily on their toes under the same conditions (fig. 5 a). Controls with both nerves and muscles crossed in the same leg always rose with the ball and toes of the foot flat against the floor, occasionally lifting the heels well off the floor, when most of the weight was on the contralateral foot (fig. 5 c).

In a further attempt to induce learning, the forelimbs of three of the experimental animals were amputated. According to Bethe ('31) dogs show a remarkable adjustment in the hind limb coordination when the front legs are amputated, an adjustment that does not occur when the limbs are only mechanically immobilized by strapping them to the sides of the body. It was hoped that some adjustment would occur in the transposed muscles when the rats became utterly dependent upon the hind legs for locomotion. Although it was extremely awkward for the animals to have to balance on the points of their heels, they never learned to contract the transposed dorsi-flexor muscles simultaneously with the extensors of the leg. Two of these rats were of a group that had been trained on the self-feeder and the other had been left for 6 months after recovery from the operation without special training. Control animals with forelimbs amputated and only two muscles left in the shank got along considerably better by balancing on the full plantar surface of the foot. The three experimental rats hobbled about without any change in the function of the transposed muscles till their deaths 7, 8 and 10 months later, respectively.

On two other of the experimetnal animals the contralateral leg was amputated about $\frac{1}{2}$ cm. above the ankle. Thus

when the rat leaned on the amputated stump in walking, the hind quarters were not as high off the floor as usual and the other leg which previously had to be raised higher than customary to prevent the plantar-flexed foot from scraping the floor (fig. 6 b), now had to be raised still higher. It was thought that the frequent catching and scraping of the foot on the floor would be a motive for inhibition of the reverse plantar flexion with perhaps a change to dorsi-flexion. Both of these animals had previously been kept without special training, one a little over 3 months, and the other about 6 months after the operation. The first was continued 3 months and then the limb with the muscle transposition was deafferented. Three weeks later the rat chewed off the deafferented foot and was sacrificed. The second animal was kept 8 months after the amputation. Neither showed any adaptive adjustment in the action of the transposed muscles.

In a last attempt to reeducate the rats, a cage was arranged in which they had to climb a vertical ladder 45 cm. high to reach food. The ladder was made of wire 2 mm. in diameter, which is thin enough to make it extremely difficult for the rats to balance with the points of their heels on the rungs. The rats climbed mostly with the front legs and since they had to hang by their paws while feeding, they tired after a few nibbles at the food and backed down to rest. This made it necessary for them to make many trips up and down the ladder for a day's meal. In clambering up and down the ladder, the rats made all sorts of movements with their hind legs and got them into all kinds of positions in and about the rungs, but they found no very satisfactory position in which much weight could be taken up by the hind limbs. Whenever the flat of the foot was placed on a rung and the animal started to shift its weight to this leg with consequent contraction of the extensor muscles, the transposed gastrocnemius muscle contracted causing dorsi-flexion of the foot at an angle so acute that any appreciable downward force applied to the foot caused it to slip off the rung. The rats never learned to rest the ball of the foot on the rungs and contract the

transposed dorsi-flexors at the same time. Control animals with only two antagonistic muscles left in the shank in normal position climbed quite easily by placing the flat of the foot on the rung and contracting the gastrocnemius, thus allowing most of their weight to rest on the hind legs. The controls with both nerves and muscles crossed in the same leg also climbed quite well by contracting the transposed dorsi-flexors synergically with the knee extensors. Of the two experimental animals, one, a bilateral case, was the youngest of the group of nine. The other was also a bilateral case but in one of the legs the lateral gastrocnemius muscle had been removed leaving only the transposed dorsi-flexors for plantar flexion. Both animals had previously been in the group of four trained for 3½ months to rise upright on their hind legs for food. The training on the ladder continued till their deaths 8 and 9 months later, respectively, without any sign of reeducation.

DISCUSSION

No adjustment, either immediate by means of automatic reflex regulation or gradual by means of a learning or conditioning process, appeared in the action of the transposed muscles in these rats.

The only functional adaptation which occurred was adjustment in the contraction of muscles left intact in normal position. For example, the rats avoided scraping the toes of the operated leg in walking, not by modifying the action of the transposed muscles, but by lifting the whole leg higher off the floor with the hip and thigh muscles, at the same time shifting more weight to the front legs. They managed to locate points about the head, neck and upper body while scratching, not by adaptive use of the transposed muscles which kept the foot extended in an unnatural position, but by adjustment of the rest of the musculature to this abnormal foot posture. There were many such adjustments on the part of the intact musculature to compensate for the reversed foot [illegible] in the action of the transposed muscles.

The absence of any immediate automatic reflex adjustment in the transposed muscles and the persistence of the reversed movement after deafferentation of the limb indicates a central nervous organization of the basic motor patterns for limb coordination. Locomotion in the rat is not the simple result of a totality of separate myotatic reflexes controlling the individual muscles of the limb according to the mechanical and postural stresses imposed on the limb structure during movement. The spinal cord must contain mechanisms for producing the organized contraction pattern of the limb musculature. Besides the apparatus for reciprocal contraction and relaxation of antagonistic muscles described by Sherrington ('06), the nerve centers must also contain a mechanism for synchronizing the contraction of shank, thigh, and hip muscles. The hind limb of the rat is generally moved as a whole, not in separate segments, and when the muscles of the shank are transposed, the rat is unable to alter the functional relationship of these muscles in the whole limb pattern. Stimuli from the periphery play upon the central mechanisms to start, stop, and modify in intensity the motor discharges to the limb, but the basic pattern of these discharges to the limb musculature depends in large part on central factors. This interpretation is in accordance with the results of studies on limb deafferentation in the rat (Sperry, unpublished) and other vertebrates (Weiss, '36 a).

In regard to the inability of the rats to correct the reversed movements by learning, it may be that rats operated at an age younger than 50 days would be more amenable to re-education after muscle transposition, though according to Liu ('28) the learning capacity of the white rat as measured with mazes is still increasing rapidly during the period from 30 to 75 days, and reaches its maximum at 77 to 100 days. According to the principles derived from the transposition of muscles in the leg of man, the transposition as performed on these rats with removal of all the other muscles acting on the same joint presents the best possible condition for learning.

After muscles for both plantar and dorsi-flexion are transposed, learning does not necessitate a dissociation of function within a group of muscles normally synergic in action as would be the case if, for example, one of the plantar flexors were left in normal position and another crossed over to produce dorsi-flexion. With the crossing of muscles for both plantar and dorsi-flexion no change in function is required either within a single agonist group of muscles or between the agonist and antagonist groups. The only change necessary is a shift in the normal functional tie-up between the shank muscles as a group and the rest of the leg musculature. Perhaps the simplest condition for learning was represented in that case in which the lateral gastrocnemius muscle was removed leaving only the dorsi-flexors to be adjusted.

Inability of the rat to modify the reversed hind foot movement as contrasted with the experience of human beings seems best attributed to the primitive condition of the rat's central nervous system. Weiss ('36 b) has shown that in amphibians, movements of the entire limb are stereotyped in relation to body movement and are not subject to learning adjustment. On the other hand, in man (Scherb, '38) the action of a single synergic group of muscles in the shank can be dissociated after muscle transposition by reeducation. There is thus an increase in capacity to modify by learning the fundamental motor patterns of limb coordination in passing from the lower to higher vertebrate forms. Clinical studies also indicate an increase in this capacity in passing from the hind limb to the fore limb in man.

Reversal of the functional relationship between the muscles of the shank and those of the rest of the limb would presuppose dissociation and reintegration of a fundamental motor pattern. Apparently, the brain processes involved in learning can deal with this pattern only as a unit. Such a unit can be combined with others in different ways to produce new behavior patterns in the gross, but finer and more extreme modifications of behavior requiring alterations of the basic units themselves, such as reversal of the inherent functional relations between

antagonistic muscles of the limb, cannot be made by the rat. Learning as observed in the behavior of the rat in mazes, problem boxes, ladders, etc., must be the result of a reassociation of these unmodifiable functional entities and higher units into new combinations and not the formation of totally new reaction patterns. The unmodifiability of these basic central nervous processes for hind limb coordination furnishes further support to the view that the process of habit formation is hierarchical in nature and involves the association of smaller units of behavior which are already organized (Weiss, '37).

SUMMARY

1. In nine rats (seven unilateral and two bilateral cases, operated at ages ranging from 50 days to 1 year) transposition of flexor and extensor muscles of the foot produced a reversal of foot movement.

2. As indicated by continued observation and moving picture study the reversal persisted in all cases with no functional adjustment, transitory or prolonged, either in common activities or in special trained performances demanding a single, slow, elementary foot movement.

3. Analysis showed that the reversal was due to clear-cut reciprocal contraction and relaxation of the transposed muscles; that mechanically the transposed muscles were capable of producing normal movement when the nerve discharges were properly timed; and that the sensitivity of the shank, ankle, foot, and transposed muscles and tendons had not been impaired by the operation.

4. A control in which the nerves were crossed instead of the muscles exhibited the same reversal of foot movement that followed muscle transposition. Controls in which both nerves and muscles were crossed in the same leg displayed, as a result of the double reversal, flexion and extension of the foot in the normal phase.

5. The nine experimental rats were kept 15½, 14½, 14, 13½, 13½, 13, 7, 6 and 5 months, respectively, after the operation. Immobilization and amputation of the contralateral hind leg,

similar transposition of muscles in the contralateral hind leg, amputation of both fore legs, training the rats to stretch upright on their hind legs for food for 3½ months as well as to climb a ladder 45 cm. high for food for 8 months, all failed to induce reeducation.

6. The unmodifiability of the elementary contraction patterns of the hind limb musculature and their persistence after deafferentation of the limb is taken to indicate a central nervous organization of the basic motor patterns for limb coordination.

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